

The effect of predator/prey density and water dynamics on feed intake and growth in spiny lobster larvae (*Jasus edwardsii*)

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Abstract

Consumption of *Artemia* by phyllosoma of the spiny lobster *Jasus edwardsii* was examined under static and turbulent conditions. Phyllosoma larvae were stocked at two densities (2 or 4 phyllosoma container⁻¹; 2P or 4P) and fed juvenile *Artemia* (1.6mm total length) at two feed rates (1.5 or 0.75 *Artemia* ml⁻¹; 1.5A or 0.75A) in 50 ml of seawater. This provided a combination of 4 treatments (2P/1.5A, 2P/0.75A, 4P/1.5A, 4P/0.75A). Daily intake of *Artemia* by phyllosoma was monitored and assessed relative to moult size and intermoult duration at differing predator-prey densities. Phyllosoma numbers were held constant; in the event of mortality, animals were replaced with others from the same cohort cultured under similar conditions. Phyllosoma endogenous reserves at hatch combined with the lowest ration of 0.75 A was sufficient to ensure normal growth and intermoult duration until Stage II. When phyllosoma were fed for an extended period (several moults), low ration and high phyllosoma density resulted in smaller size and extended intermoult duration. Fluctuations in the feeding pattern of phyllosoma were evident between treatments during the experiment. Phyllosoma with access to more *Artemia* consumed more, and consumption was reduced prior to a moult, even during early stages of development. The second phase of the study examined the intake of 1.7 mm juvenile *Artemia* by phyllosoma and their response to flow-induced turbulence with a combination of two water exchange rates (2.5 or 5 times h⁻¹) and two inlet positions (2 cm above the water surface or 0.5 cm above the culture vessel bottom and parallel to it). Larvae exposed to slow flow were larger and had a shorter intermoult duration associated with an increased ability to capture and consume more *Artemia*. Similar numbers of *Artemia* were consumed during the intermoult in high flow treatments compared to the low flow, albeit over a longer duration. Phyllosoma development between moults required less *Artemia* to be consumed under static conditions.

Key words: *Jasus edwardsii*, water turbulence, density, flow rate, feed intake, intermoult duration.

Introduction

The key to sustainable aquaculture of spiny lobsters needs to be based on the successful and consistent hatchery production of juveniles (Ritar et al. 2002). Spiny lobster phyllosoma have the longest and most complex larval history of all decapod crustaceans, involving at least 9 distinct morphological stages and up to two years to metamorphosis as a puerulus; the pre-juvenile phase (Kittaka, 2000). The larval culture requirements for spiny lobsters, including *Jasus edwardsii*, *Panulirus japonicus* and *Panulirus ornatus* are currently under investigation (Matsuda and Yamakawa, 1997; Matsuda, et al. 2003;

Bourne et al. 2004; Smith et al. 2003, 2004, Smith and Ritar, 2006) with complete larval development to metamorphosis reported in five species (Kittaka, 2000). However, to date larval rearing to the puerulus stage has only been achieved on an experimental scale, with considerable work still required to attain the goal of commercial production. At present the standard diet for larval rearing of phyllosoma is based on ongrown disinfected *Artemia* (Smith and Ritar, 2006), because no suitable artificial diets are available. Therefore, it is important to optimize phyllosoma growth while minimizing *Artemia* production, a time-consuming component of culture.

The interaction between phyllosoma and *Artemia* and their ability to respond to differing water flow dynamics have important implications for the production of fast growing healthy larvae and may help set the focus for future designs of culture systems. To date, *J. edwardsii* phyllosoma larvae have been cultured in an array of vessels with distinctly different flows, including static beakers, tubs with circular horizontal flow, vessels with upwelling turbulence and planktonkriesels (Illingworth, 1997; Kittaka, 2000; Ritar, 2001; Smith et al. 2003).

The aims of this study were to assess optimal feeding regimes, the influence of flow-induced turbulence on the feeding ability of early stage phyllosoma, and to provide a focus for future system design. The *Artemia* consumption per phyllosoma, the intermoult duration, and the size and survival of phyllosoma were measured as treatment responses.

Materials and Methods

Artemia production

Artemia cysts (INVE, Great Salt Lake Prime Gold) were hatched in 50 l white fibreglass cones. All hatching and culture of *Artemia* were conducted using aerated, 1 μ m filtered ozonated seawater, maintained at $34 \pm 1\%$ and $28 \pm 1^\circ\text{C}$. At hatch (24 h) *Artemia* nauplii were harvested, rinsed with freshwater and cultured at an initial density of 10 ml^{-1} in 800 l cones. *Artemia* were fed the micro-alga *Chaetoceros muelleri* at a cell density 2×10^5 cells ml^{-1} in the culture vessel; algal feeding was supplemented with rice pollard. Culture cones underwent partial harvests on days 4 through 6 to provide daily feed requirements. Phyllosoma were fed 1.6 and 1.7mm juvenile *Artemia* daily during Experiment 1 (total - 5 400 *Artemia* day^{-1}) and 2 (total - 40 800 *Artemia* day^{-1}), respectively. Prior to feeding to phyllosoma *Artemia* were purged with axenic *C. muelleri* and formalin ($400 \mu\text{g g}^{-1}$) for 60 min to reduce the bacterial content of the food source (Smith and Ritar, 2006).

Experiment 1: Predator – Prey interaction

Larval selection and culture conditions

Newly hatched phyllosoma were obtained from ovigerous broodstock caught off Flinders Island on Tasmania's north-east coast ($40^\circ 32' \text{S}$, $148^\circ 16' \text{E}$) in June, and maintained at the Marine Research Laboratories in Taroona until hatch during September. Larvae were cultured in 70 ml clear plastic sample jars containing 50ml of ozonated, UV treated, filtered seawater (1 μ m filtered, $34 \pm 1\%$) gently agitated by air bubbling from an open airline (1 bubble sec^{-1}). Phyllosoma larvae were stocked at two densities (2 or 4 phyllosoma jar^{-1} , respectively) and fed 1.6 mm *Artemia* at either 1.5 or 0.75 *Artemia* ml^{-1} (75 or 38 *Artemia* jar^{-1} respectively, Table 1). All treatments were conducted in quadruplicate. Additional phyllosoma were maintained in 1 l beakers at the same predator-prey densities to supply replacement phyllosoma in the event of treatment mortality, thus maintaining consistent densities throughout the experiment. Growth of replacement

phyllosoma was homogeneous and representative of that attained in individual treatments. During the study, between 25–50% of animals were replaced due to deaths, with substitutions primarily in the first 3 days of the study and at the moult to Stages II and III. Jars containing *Artemia* without phyllosoma (“blanks”) were maintained to assess mortality unrelated to phyllosoma predation, and these mortalities were subtracted from the other treatments. Sample jars and replacement beakers were maintained at 18°C and randomly suspended within a recirculating temperature control water bath. All culture containers were 75% immersed in the heated water with unimpeded flow to the sides and bottom of the containers. During daylight hours, light was $0.05 \mu\text{mol m}^{-2} \text{s}^{-1}$ on a 12:12 (light:dark) photoperiod cycle. Complete water exchanges were conducted daily at 11am to facilitate the counting of remaining whole and partial/dead *Artemia*, remove moults, replace dead phyllosoma and to conduct phyllosoma measures.

Phyllosoma feeding

Phyllosoma larvae were fed their *Artemia* ration daily by 1 pm and for a minimum duration of 22 h. In all treatments, *Artemia* were individually counted into culture jars. *Artemia* numbers for phyllosoma held in 1 l beakers as replacements were determined volumetrically. At the completion of the feed period, the numbers of live *Artemia* plus those dead or partially eaten were counted in each treatment jar and total *Artemia* consumption was calculated. Due to low numbers of dead *Artemia* in the ‘blank’, and the majority of dead/partial *Artemia* being predominantly whole, only missing *Artemia* were calculated as contributing to the consumption total.

Post water exchange and feeding, antibiotics (oxytetracycline hydrochloride 25ppm, Engemycin 100, Intervet, Australia) were added to all replacement beakers. Antibiotics were used to primarily reduce the impact of filamentous bacterial fouling on phyllosoma and remained as a continuous bath until flushed the next day during water exchange.

Monitoring growth and intermoult duration

Total body length (anterior tip of the cephalic shield to the posterior point of the abdomen) was measured on 20 newly-hatched Stage I phyllosoma and the subsequent 2nd, 3rd, 4th and 5th developmental stages on days 13, 25, 37 and 49, respectively, as described by Lesser (1978). Measurements were obtained using an overhead projection microscope (Nikon 6C profile projector, 20 times magnification). The pattern of phyllosoma moulting was recorded daily with the intermoult duration calculated as the mean period for 50% of animals to moult from one stage to the next in individual replicates. Phyllosoma culture was conducted for 49 d, sufficient for the most advanced treatments to attain Stage V of larval development.

Experiment 2: Effect of flow on Artemia consumption

Larval selection and monitoring

Phyllosoma larvae were stocked at a density of 40 l^{-1} into quadruplicate 1.6 l plastic flat-bottomed beakers and cultured to Stage IV (38 d after hatch). All beakers were fed $1.74 \pm 0.03 \text{ mm}$ *Artemia* at a rate of $1.5 \text{ ml}^{-1} \text{ day}^{-1}$; the same phyllosoma *Artemia* density ratio as 2P/1.5A in the first study. *Artemia* numbers for daily feeds were determined volumetrically after the average of three 75 ml sub samples of freshly harvested/purged *Artemia* was taken. Phyllosoma larvae were fed *Artemia* by 1 pm and left to feed overnight. Each morning at 11am, larvae were removed and placed in fresh containers and the consumption of *Artemia* assessed. Phyllosoma survival was monitored every second day with the average used to calculate consumption on intermediate days. Phyllosoma had a minimum daily feeding duration of 22 h before *Artemia* consumption was assessed. The

difference between the number of *Artemia* fed at time 0 and those remaining (alive, dead/partial) were presumed eaten. *Artemia* were additionally cultured without phyllosoma (blanks) to assess mortality unrelated to feeding, mortality was < 2%; thus no adjustments were made to consumption calculations during this component of the study. The monitoring of phyllosoma size and intermoult duration remained as previously described. Survival was recorded on days 13, 25 and 38 corresponding to Stages II, III and IV, respectively.

Larval culture conditions

Phyllosoma were subjected to water turbulence in the beakers produced by two inlet positions, either top (2 cm from the water surface and near the side) or bottom (0.5 cm from the beaker bottom, parallel and directed diagonally across it), and two water flow rates, either slow (2.5 exchanges h⁻¹) or fast (5 exchanges h⁻¹). Thus for:

- a top inlet and a slow flow rate, water was evenly dispersed throughout the beaker water column without producing a dominant top to bottom circular current.
- a bottom inlet and slow flow rate, water was dispersed in a horizontal action on the beaker floor, with mixing extending slowly into the upper layers.
- a top inlet with fast flow rate, water moved in a turbulent circular top to bottom current, evenly mixing the water column.
- a bottom inlet with fast flow rate, water moved turbulently across the beaker floor then upwards at the opposite side of the beaker towards the water surface, producing a rapid bottom to top circular movement.

Water supply to the larval rearing system was flow-through, filtered to 1 µm, ozonated as described by Ritar et al. (2006) and temperature controlled at 18 ± 1°C (heat/chill units, APAC CO10PHH7AA, Airco, Hobart, Australia). Light was provided at 0.05 µmol m⁻² s⁻¹, measured at the water surface on a 12:12 (light:dark) photoperiod cycle. The lighting system comprised a series of fluorescent lamps positioned 2 m above the culture containers fitted with covers underneath the lamps to provide a reflected diffused lighting source. *J. edwardsii* phyllosoma are strongly photopositive for the first 1 – 2 days post-hatch, thereafter they display minimal phototactic response.

Statistics

Statistical analyses were conducted using multifactor analysis of variance with Tukey-Kramer HSD tests for post-hoc comparison. Arcsin√ transforms were performed on percentage data. $P < 0.05$ was considered significantly different (Sokal & Rohlf, 1995). Data are presented as mean ± SEM. Statistics were executed using JMP version 3.1. (SAS Institute Inc.).

Results

Experiment 1: Predator-prey density

Growth and intermoult duration

There was no significant effect of phyllosoma or *Artemia* density on total length at Stage II (Fig. 1). Phyllosoma stocking density and interactions with *Artemia* density significantly affected the total length of Stage III phyllosoma. This effect was accentuated with culture to Stage IV, with animals in the highest phyllosoma density and fed the least *Artemia* (4P/0.75A) being significantly smaller than all other groups.

Phyllosoma intermoult duration followed a similar pattern to that of total length. The intermoult duration of Stage I phyllosoma (between hatch and the first moult) was

unaffected by treatment conditions (Fig. 2). The intermoult duration of Stage II phyllosoma (duration between Stage II and III moults) and subsequently Stage III phyllosoma (duration between Stage III and IV moults) were longer in the combination of high phyllosoma and low *Artemia* densities. By day 49, all phyllosoma in treatment 2P/1.5A had completed the moult to Stage V, whereas treatments 2P/0.75A and 4P/1.5A were 62.5 and 75% complete, respectively, while 4P/0.75A had only just completed the moult to Stage IV and had not commenced the moult to Stage V (Fig. 3).

Artemia consumption

There were several distinctive patterns of daily *Artemia* consumption (Fig. 3). The greatest number of dead/partial *Artemia* occurred at the highest *Artemia* to phyllosoma ratio (2P/1.5A). Almost all available *Artemia* were consumed on a number of occasions in the lowest *Artemia* to phyllosoma ratio (4P/0.75A). *Artemia* consumption declined markedly in all treatments once or twice during an intermoult period, and always immediately prior to a moult event.

The proportion of the total *Artemia* eaten per phyllosoma increased as the amount of food available became more limited (Fig. 3). Consequently, a similar reduction in dead/partial *Artemia* was also exhibited. An increase in phyllosoma density and reduced *Artemia* density resulted in minimal amounts of partial/dead *Artemia* remaining.

Artemia consumption was significantly affected by phyllosoma and *Artemia* density. Treatment 2P/1.5A, with the highest *Artemia* to phyllosoma ratio of 37.5 *Artemia* per phyllosoma, consistently showed greater numbers of *Artemia* consumed per stage and cumulatively for all three stages (Fig. 4). In the treatments where the ratio of *Artemia* to phyllosoma were the same (2P/0.75 and 4P/1.5A, 18.75 *Artemia* available per phyllosoma), consumption within each stage remained equivalent, although cumulative consumption (Stages I, II and III) was higher where *Artemia* density was greater (4P/1.5A). High phyllosoma density coupled with low *Artemia* density (4P/0.75A) resulted in the lowest cumulative total *Artemia* consumption for stages I, II and III (Fig 4).

Experiment 2: Effects of flow and inlet positioning

Growth, survival and intermoult duration

Survival to Stage IV was variable between replicates, thus no significant effect of either flow or positioning was noted. At the completion of the study, survival was 68.2 ± 7.9 % for the bottom slow treatment, and 42.7 ± 2.8 % for the bottom fast treatment. The top slow and top fast treatments attained intermediate levels of survival of 54.2 ± 8.9 % and 53.1 ± 5.9 %, respectively. Flow had a significant effect on size, with Stage IV phyllosoma significantly larger in the top slow and bottom slow treatments (5.05 ± 0.04 and 5.05 ± 0.03 mm, respectively) compared to those in the top fast and bottom fast treatments (4.74 ± 0.02 and 4.68 ± 0.04 mm, respectively).

There was no significant effect of flow or positioning on the duration of Stage I (period from hatch to the moult to Stage II, Fig. 5). However, the duration of the Stage II (period from the Stage II moult to the Stage III moult) was shortest in the top slow treatment while those in the bottom fast were the longest, with bottom slow and top fast demonstrating intermediate durations. Stage III (period from the Stage III moult to the Stage IV moult) was shorter in the slow flow treatments compared to those in the fast flow treatments. This was further demonstrated in the total culture duration from hatch to the completion of Stage III (moult to Stage IV), with a minimum of 32.9 days in the top slow treatment and a maximum of 37.3 in the bottom fast treatment.

Artemia consumption

There were a number of minor differences in the phyllosoma Stage-specific *Artemia* consumption (Fig. 6). Stage I phyllosoma in the bottom-slow treatment consumed more *Artemia* than all other treatments, while Stage II phyllosoma from the top-slow treatment consumed more than those from the top-fast treatment. *Artemia* consumption during Stage III, and also the cumulative total of Stages I, II and III, did not differ significantly between treatments. Inlet positioning did not have a significant effect on consumption. *Artemia* consumption by phyllosoma followed the same pattern as in Experiment 1, with one-two peaks in consumption mid-stage, reduced consumption prior to a moult, and increased post-moult regardless of treatment, albeit at lower levels over a significantly longer time-frame for fast flow treatments (Fig. 7). It is worth noting that more *Artemia* were consumed to attain Stage IV of development when exposed to slow turbulence in the second study (593.8 ± 5.8 *Artemia*), compared to the same treatment under static conditions in the first study (Treatment 1 – 2P/1.5A; 521 ± 9.7 *Artemia*) even though the duration to Stage IV was the same.

Discussion

J. edwardsii phyllosoma typically have a 10-12 day intermoult duration between hatch and the moult to Stage II, with a point-of-no-return for commencement of feeding of 4 days, therefore they have limited endogenous reserves (Abrunhosa and Kittaka, 1997). Even at the minimum *Artemia* feed ration there was no influence on phyllosoma size or intermoult duration at Stage II. The minimum ration was adequate, while excess reserves from larger rations may have been stored for use during later stages (Mikami and Takashima, 1993). When insufficient feed is provided, moulting may be delayed by a number of days (Tong et al. 1997). When feed is not available, reserves are depleted, phyllosoma do not moult and death from starvation occur 12-20 days post-hatch (Tong et al., 1997; Smith et al. 2003). When phyllosoma were fed for in excess of 45 days, those fed the lowest numbers of *Artemia* were smaller with longer intermoult durations; they were just completing the moult to Stage IV while all other groups had commenced the moult to Stage V. Vijayakumaran and Radhakrishnan (1986) also noted substantial moult delays in *Panulirus homarus* phyllosoma when fed lower *Artemia* rations, with the lowest ration not moulting at all while others undergoing intermediate stages of development rather than direct moulting to the next morphological stage. It may be that longer intermoult durations between stages are a prelude to additional instars. During our study we did not record additional instars suggesting that the lowest feed rate supports a normal moulting pattern, albeit somewhat delayed.

Phyllosoma with access to the greatest number of *Artemia* consumed more, which is common in crustacean culture, and may provide reserves for use during later stages (Inoue, 1965; Vijayakumaran and Radhakrishnan, 1986; Tong et al. 1997, 2000; Thessalou-Legaki et al. 1999). The significance of a carryover of reserves has been noted previously (Mikami and Takashima, 1993) and can positively affect size and reduce intermoult duration. Phyllosoma are active predators, able to locate, catch and consume *Artemia* even at low densities, although at high density there is an increase in the frequency of chance encounters contributing to consumption (Thessalou-Legaki, et al. 1999). Thus, under the influence of high prey densities the importance of active foraging by phyllosoma is reduced and may assist in the conservation of energy stores.

Where two treatments had the same phyllosoma/*Artemia* ratio (4P/1.5A and 2P/0.75A), total *Artemia* consumption was greatest where prey density was highest (4P/1.5A), irrespective of phyllosoma number. Prior to this study, the interactions between phyllosoma at low density and their food source, *Artemia*, were unclear (Smith and Ritar,

2006). This study suggests, at least during early development, that interaction between phyllosoma plays a lesser role in reducing intake than does access to food, and reinforces the suggestion by Tong et al. (1997) that prey capture is related to prey density.

The use of small juvenile *Artemia* during our study allowed clear differentiation of daily intake across all feed treatments. The reduction in feeding prior to the moult was a prominent feature observed during all stages, previously only reported for more advanced phyllosoma (Tong et al. 1997). In treatments where food was limiting, i.e. 4P/0.75A, there were very few dead/partial *Artemia* remaining. Whole *Artemia* may have been consumed during initial feed encounters, although it is likely that phyllosoma returned to dead/partials after the majority of live feed had been eaten.

Comparison between the consumption by *J. edwardsii* phyllosoma in static culture in our study with that of Tong et al. (1997) highlights the significance of *Artemia* size. During our study greater numbers of smaller *Artemia* were consumed per day, equating to approximately 75% of the biomass consumed in the Tong et al. (1997) study. This suggests that increased effort is required to capture a similar biomass of smaller *Artemia* when animals are fed to satiation. When the optimal intake can not be attained, the moult interval is lengthened and the moult increment is reduced (Vijayakumaran and Radhakrishnan, 1986). Tong et al. (2000) found a similar pattern of time-limiting capture ability when examining the consumption of 1 mm and 2-3 mm *Artemia*. So not only does the density of *Artemia* affect the ability of phyllosoma to catch prey, but also, the size of *Artemia* impacts on the biomass of food consumed.

During early stages of development (Stages I-IV), we noted that phyllosoma were unable to swim in the 'typical' circular feeding pattern when exposed to constant turbulence experienced in the fast treatments, and instead were swept along with the prevailing current. Phyllosoma in the slow treatments caught a greater number of *Artemia* per day in the absence of constant turbulence, both phyllosoma and *Artemia* were located on the jug bottom, except for the first 1 - 2 days when phyllosoma may be phototactic and actively swim to the surface of the container. The result of increased food consumption and reduced capture effort by phyllosoma in slow treatments produced larger animals in a shorter time, and perhaps a store of energy for sustenance during periods of low food availability. This may be a strategy to optimise their chance of survival during their extended planktonic life-phase. To the contrary, phyllosoma in the fast treatments caught less *Artemia* per day and endured a longer intermoult period to attain the same stage of development, albeit at a smaller size. While restricted intake reduced growth and increased the intermoult period there were no additional instars (moult phase whereby growth occurs without a change in morphology) as noted by Vijayakumaran and Radhakrishnan (1986).

During this relatively short study we noted that constant turbulence impeded phyllosoma from capturing *Artemia* while previously in studies of longer duration slow flow or no flow has been associated with fouling; due possibly to organisms clumping together while feeding (Smith unpublished). This creates a paradoxical situation whereby some turbulence is desirable to reduce adverse phyllosoma interaction and facilitate predator-prey mixing, while excess turbulence reduces food intake. Therefore, we are currently investigating the use of intermittent turbulence within suitably designed culture vessels; a pulse of incoming water facilitates predator-prey mixing interspersed with static periods to facilitate prey capture and feeding opportunities.

The provision of larger *Artemia* may also improve phyllosoma growth and survival by improving the feed efficiency of capture events. Large *Artemia* have a reduced tendency to swarm and assume a homogeneous distribution (Gulbrandsen, 2001) that may assist in their capture.

Conclusion

In summary, the provision of suboptimal amounts of diet to phyllosoma manifests itself in reduced phyllosoma size at subsequent moults and a longer intermoult duration. By increasing *Artemia* density there is a concomitant increase in their consumption by phyllosoma. During phyllosoma development, constant high water turbulence should be avoided to allow capture of *Artemia*. Future improvements in culture vessel design should incorporate optimum water flow dynamics for the distribution of predator and prey to maximise feeding opportunities.

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Table 1. Phyllosoma and *Artemia* treatment parameters (Experiment 1).

Treatment	Phyllosoma number	Artemia density ml⁻¹	<i>Artemia</i> available per phyllosoma	Phyllosoma density l⁻¹
1 – 2P/1.5A	2	1.5	37.5	40
2 – 4P/1.5A	4	1.5	18.75	80
3 – 2P/0.75A	2	0.75	19	40
4 – 4P/0.75A	4	0.75	9.5	80

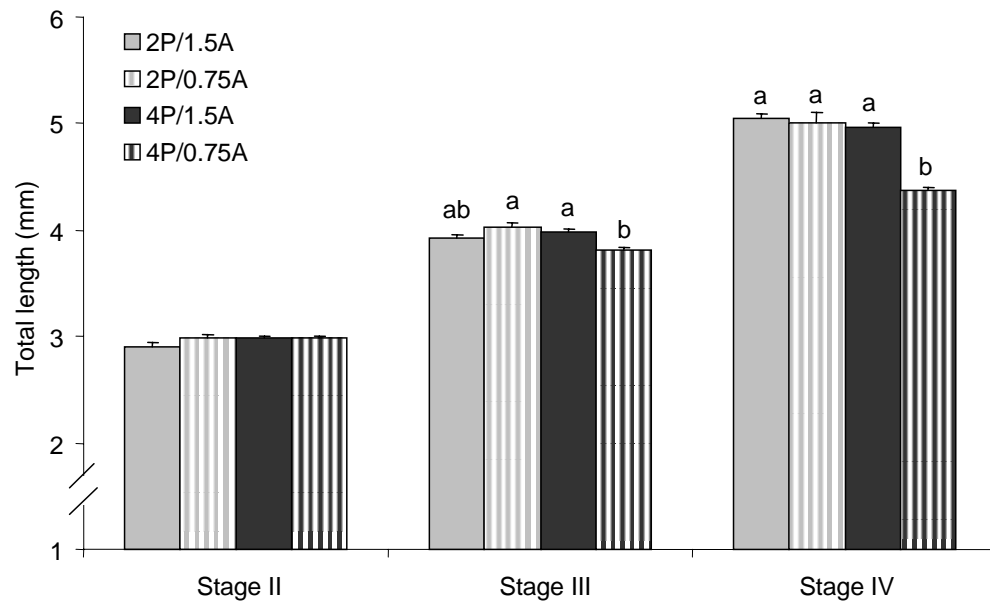


Fig. 1. Total length (mm) of phyllosoma at Stages II, III, and IV. Treatments were a combination of predator density (2 or 4 phyllosoma) and prey density (1.5 or 0.75 *Artemia* ml⁻¹), designated as 2P/1.5A, 4P/1.5A, 2P/0.75A or 4P/0.75A in 50 ml of water in quadruplicate. Different letters denote a significant difference in phyllosoma length within a stage.

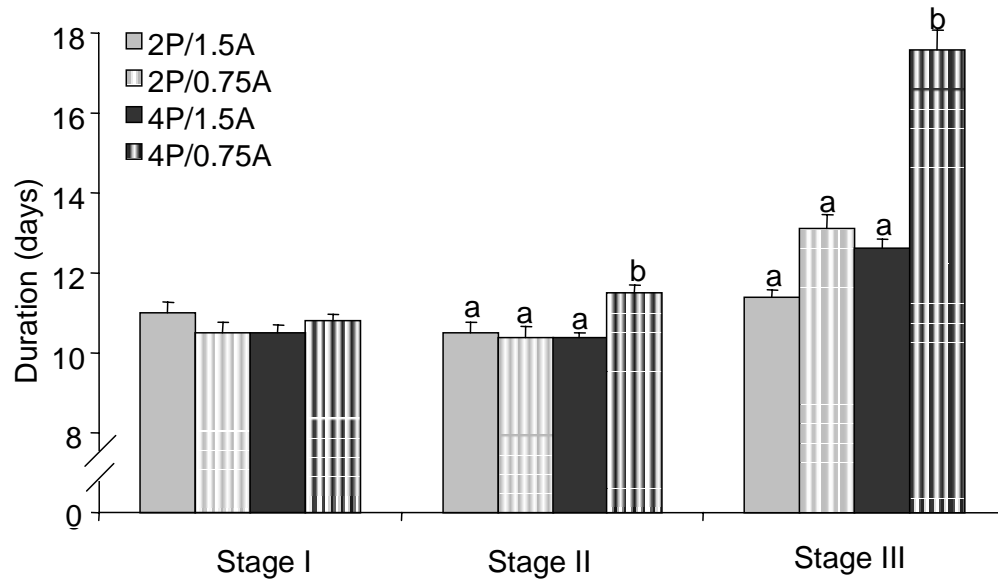


Fig. 2. Intermoult duration for Stage I, II and III phyllosoma. Treatments were a combination of predator density (2 or 4 phyllosoma) and prey density (1.5 or 0.75 *Artemia* ml⁻¹), designated as 2P/1.5A, 4P/1.5A, 2P/0.75A or 4P/0.75A in 50 ml of water in quadruplicate. Different letters denote a significant difference in intermoult duration within a stage.

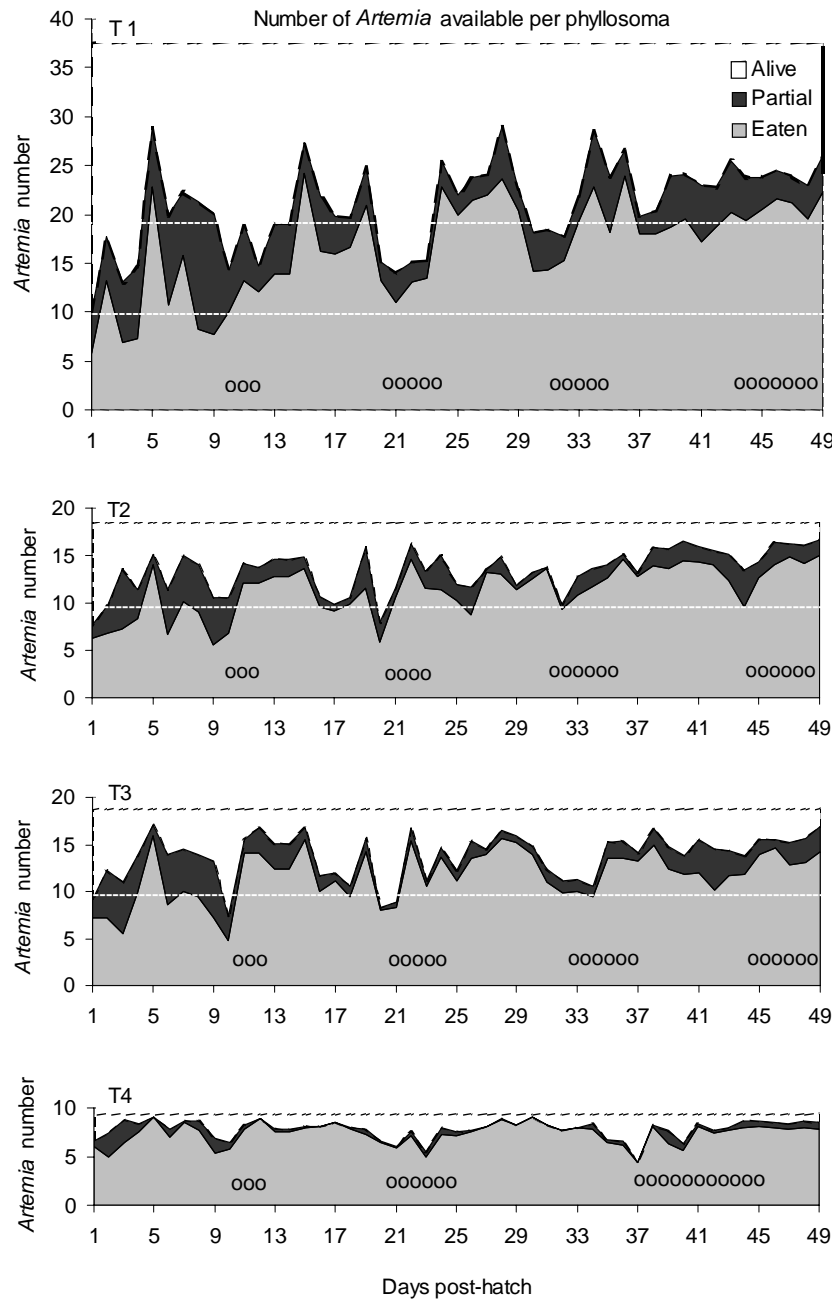


Fig. 3. Pattern of daily *Artemia* consumption by phyllosoma. Treatments were a combination of predator density (2 or 4 phyllosoma) and prey density (1.5 or 0.75 *Artemia* ml⁻¹), designated as 2P/1.5A, 4P/1.5A, 2P/0.75A or 4P/0.75A in 50 ml of water in quadruplicate. Grey shaded regions illustrate the number of *Artemia* eaten, black shaded regions represent partial or dead *Artemia* and white regions were live *Artemia*. Black broken lines illustrate the maximum number of *Artemia* available per phyllosoma, the white broken lines demonstrate maximum *Artemia* availability in other treatments. The circles near the horizontal axes of each graph are an indication of the timing and duration of the moults. Note that 4P/0.75A underwent three moults attaining Stage IV, while the other treatments had completed or commenced the fourth moult to Stage V.

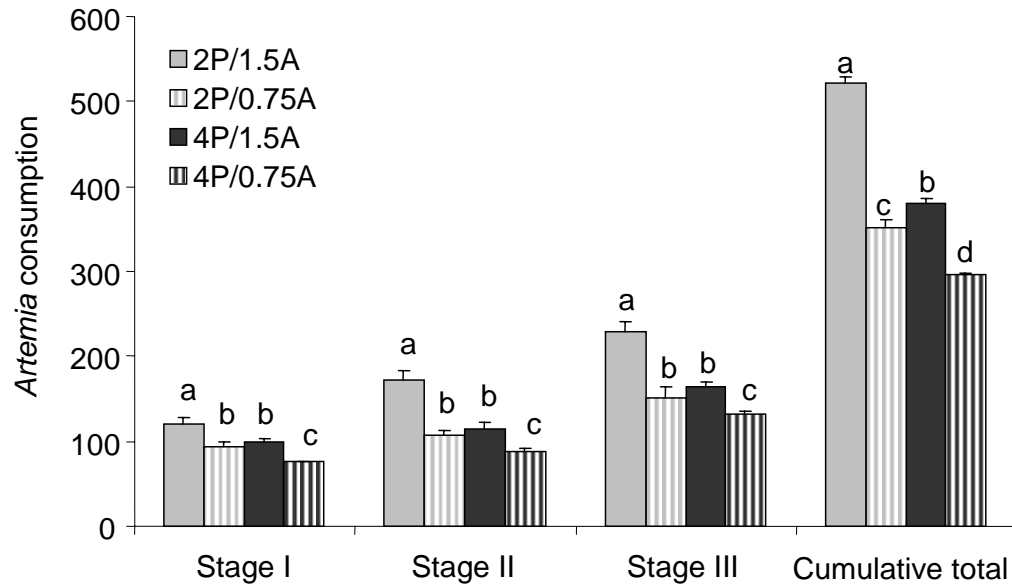


Fig. 4. Number of *Artemia* consumed by phyllosoma during each stage and the cumulative total consumption during Stages I, II and III. Treatments were a combination of predator density (2 or 4 phyllosoma) and prey density (1.5 or 0.75 *Artemia* ml⁻¹), designated as 2P/1.5A, 4P/1.5A, 2P/0.75A or 4P/0.75A in 50 ml of water in quadruplicate. Different letters denote a significant difference in *Artemia* consumption within a stage.

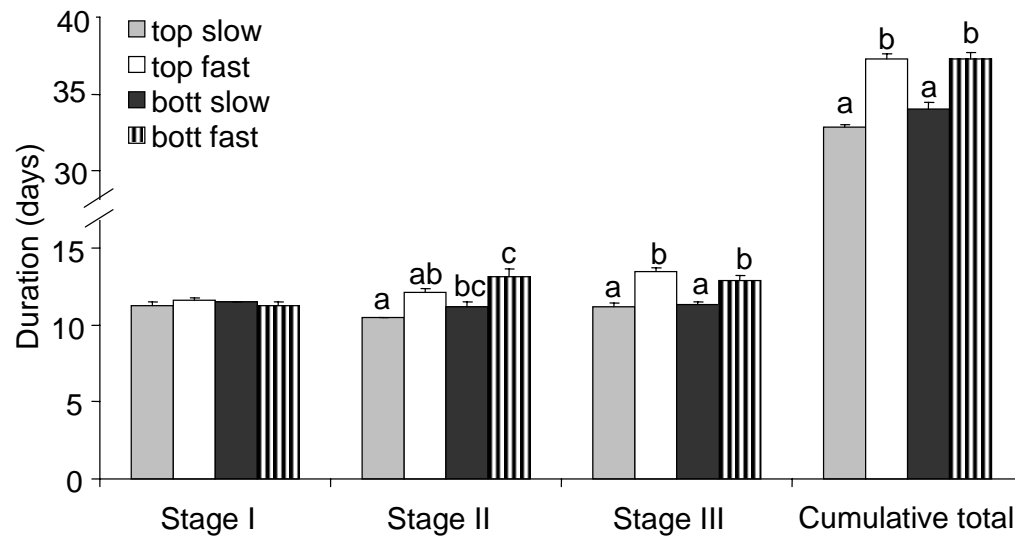


Fig. 5. Duration of each phyllosoma stage and the cumulative total duration of Stages I, II and III. Treatments were a combination of different water inlet positions of top (2 cm above the water surface) or bottom (0.5 cm above the beaker bottom and parallel to it) and water flow rates of slow (2.5 exchanges h^{-1}) or fast (5 exchanges h^{-1}). Different letters denote a significant difference in intermoult duration within a stage.

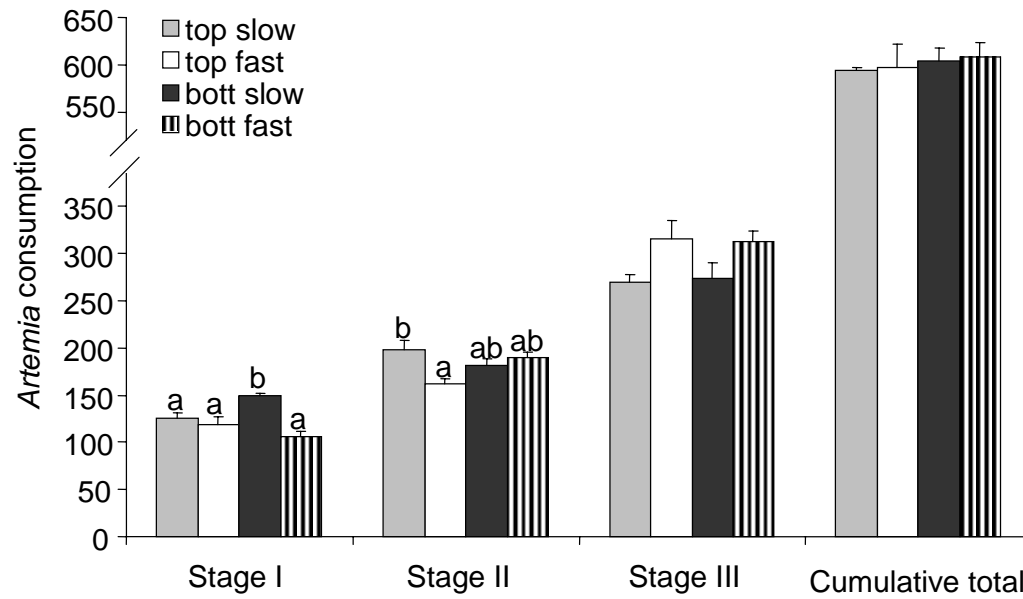


Fig. 6. Number of *Artemia* consumed by phyllosoma during each stage and the cumulative total consumption during Stages I, II and III. Treatments were a combination of different water inlet positions of top (2 cm above the water surface) or bottom (0.5 cm above the beaker bottom and parallel to it) and water flow rates of slow (2.5 exchanges h^{-1}) or fast (5 exchanges h^{-1}). Different letters denote a significant difference in *Artemia* consumption.

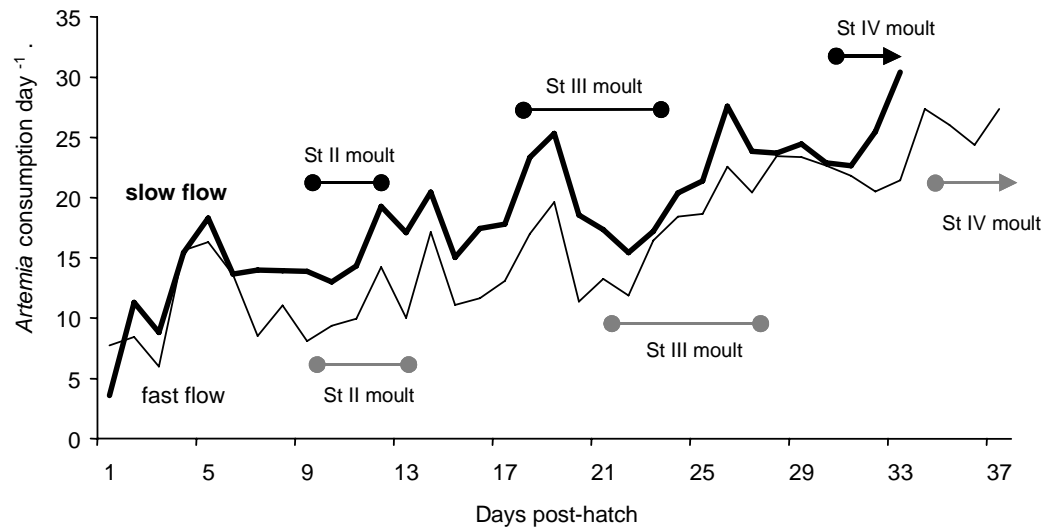


Fig. 7. Pattern of daily *Artemia* consumption by phyllosoma. There was no significant effect of inlet position on consumption therefore data was pooled for fast and slow-flow treatments. The timing and duration of moulting is noted by horizontal bars at Stages II, III and IV (black: slow flow; grey: fast flow).